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FORREST SHREVE

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The Plant World Association

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THE RESISTANCE OFFERED BY LEAVES TO TRANSPIRATIONAL WATER LOSS¹

BURTON EDWARD LIVINGSTON

The Johns Hopkins University, Baltimore, Md.

INTRODUCTION

The rate of water loss from plant surfaces exposed to the air is always lower than the rate of evaporation from an equal area of water surface in the same surroundings. Usually the evaporation rate is very many times as great as is that of transpiration,² and it is thus possible to regard plant tissues as exerting a retarding influence upon evaporation and outward diffusion of their contained water. This retarding influence, or resistance to transpirational water loss, is of different magnitude for different plant forms, and for the same form grown under different conditions, also for different portions of the transpiring surface of the same individual plant. Furthermore, for the same plant, and for the same portion of its surface, the resistance to transpiration often varies with the age of the organism and with the diurnal march of various internal conditions. Obviously, the factors which condition the retarding influence here considered are all to be characterized as internal, that is, they are all operative within the periphery of the plant body, though they must of course be ultimately controlled by external conditions, either in the present or in the past. In the broad sense, these factors are anatomical; in physical terms, they depend on the nature, amount and arrangement within the plant body, of its various component substances.

¹ Botanical Contribution from the Johns Hopkins University No. 28. A preliminary announcement of the direct method here used was published in Notes from the Botanical Laboratories, The Johns Hopkins University Circular, pp. 11-13, February, 1912.

² Livingston, B. E., The relation of desert plants to soil moisture and to evaporation. Publication 50 of the Carnegie Institution, 1906.

Thus, for example, the resistance to water loss by transpiration is much greater in leaves having a well developed cuticle than in others in which the cuticular layer is thin or absent. Also, other internal conditions being equal, a leaf with closed stomatal pores must exhibit a greater retarding influence upon water loss than one with open pores. Many other examples might be mentioned.

It is clear that an adequate appreciation of the dynamics of the water relations of plants, and especially of the transpiration process, must rest not only upon a quantitative knowledge of the influence of external conditions on the transpiration rate, but also, upon just as quantitative and thoroughly physical a knowledge of the causal relations obtaining between internal factors and this rate of water loss. We require measurements of the water-extracting power of the aërial environment and corresponding measurements of the transpirational retardation which is effective within the plant.

By the use of the various atmometers which are now available,³ it is possible somewhat readily to measure and integrate the environmental water-extracting power for any locality and for any time period, providing freezing of water does not occur.⁴ This instrument gives at once a generalized estimate of the environment above the soil surface, as far as this influences water removal. We are thus fairly well equipped to attack problems dealing with differences in the external conditions.

Our status is, however, not nearly so satisfactory when we face problems of differences in the internal factors. In attempting to deal with variations and differences in transpirational retardation, as this is manifested in different plant forms and in the same form at different times, advantage has been taken of a mathematical treatment of the problem, which is common in physical analyses. This relies on the principle that, wherever two, and

³ Livingston, B. E., A rotating table for standardizing porous cup atmometers. *Plant World* 15: 157-162, 1912; and the literature there referred to. Also see: Livingston, Grace J., An annotated bibliography of evaporation. *Monthly Weather Review*, 1908-1909.

⁴ For the most part, the problems of plant transpiration do not require the measurement of the evaporating power of the surroundings during freezing periods; nevertheless an adequate method should be devised for such times.

only two, conditions are known to influence the time rate of a given process, this rate must be proportional to the product of the effective intensities of the two conditions. If, then, it be possible to determine experimentally one of the effective intensities, as well as the rate of the resulting process, it is not necessary to measure the other, which may be derived by simple division.

In the study of transpiration, the method of the relative transpiration ratio⁵ is founded upon the principle just stated, the primary assumption being that the absolute transpiration rate is proportional to the product of the intensity of the evaporating power of the surroundings and the magnitude of the transpiring power of the plant. This transpiring power is of course the reciprocal of the resistance manifested by the plant, to water loss by transpiration. It is assumed, to be more specific, that, if a plant with a superficial area of p loses m grams of water during a time period when an atmometer with similar exposure loses r grams, and if another plant with area q loses n grams while the same, or a similar, atmometer loses s grams, then the internal conditions favoring water loss from the first plant are to those of the second as $\frac{m}{pr}$ is to $\frac{n}{qs}$. The ratio of the loss from the plant, per unit area, to the loss from the standard atmometer, under the same conditions, is proportional to the transpiring power of the plant. This ratio really states the number of atmometers that would be necessary to evaporate as much water as unit area of the plant, the instrument and plant being similarly exposed for the same time period.

Where the problem in hand contemplates only variations in the transpiring power, or its reciprocal the resistance factor, for the same plant, and at different hours of the same day, it is unnecessary to introduce into the computation the area of the plant, this area being assumed to be sensibly constant. Thus, if the

⁵ Publication 50 of the Carnegie Institution, 1906; also see: Livingston, B. E., Relative transpiration in cacti, *Plant World*, 10: 110-114, 1907.

Delf, E. M., Transpiration and behavior of stomata in halophytes. *Ann. Bot.* 25: 485-505, 1911.

Idem, Transpiration in succulent plants. *Ibid.* 26: 409-441, 1912.

transpirational loss from a plant be m for one time period and n for another, and if the loss from the atmometer, under the same surroundings and for the same time periods, be r and s , respectively, then the intensity of transpirational retardation for the first period is to that of the second as $\frac{r}{m}$ is to $\frac{s}{n}$ or the resistance to

water loss is $\frac{ms}{nr}$ times as effective during the second period as during the first. In the study of the daily march of the property which we are considering, it is convenient to adopt as unity the value corresponding to one of the short periods of observation, and to reduce the other values to this basis by division.

Much as the method of the relative transpiration ratio has aided in the advance of our knowledge of the physics of transpiration and of the conditions limiting plant life, it is at best but a very indirect and cumbersome means for comparing transpirational retardations. It requires the absolute transpiration rates and the corresponding atmometric data, the weighing of potted plants or the reading of potometers, together with the operating of atmometers. It is thus not well suited to the estimation of physiological resistance to transpiration in the field. A more direct method has therefore been attempted. A description of this and a statement of some of the results thereby obtained, form the purpose of the present paper.

The work here reported was begun in the summer of 1908, in the laboratories of the *Pflanzenphysiologisches Institut* in Munich, where facilities for experimentation were kindly placed at the disposal of the writer by the Director, Prof. K. von Göbel. Studies along this line have been prosecuted at intervals since that time, but the most satisfactory advances were made in the summer of 1911, at the Desert Laboratory of the Carnegie Institution. Here it was the author's pleasure to have the valuable assistance of Mr. J. S. Caldwell, in this and related lines of study. In the summer of 1912, at the same Laboratory, comparisons of the transpiring power of different plants were carried further, with the assistance of Mr. E. M. Harvey.

A METHOD FOR COMPARING TRANSPIRATIONAL RETARDATION

The tendency of water to evaporate from a free surface depends upon two sets of conditions, one internal, resulting in the vapor tension of the surface, and the other external, the evaporating power of the supernatant air. The vapor tension is conditioned by several factors, such as the temperature of the surface, the amount of dissolved material in the water, etc. Now transpirational retardation in plants may be compared to the retardation of evaporation from a solution, caused by the presence of solutes. This suggests that the problem of comparing transpirational retardations involves the finding of some sort of hygrometric device, which may indicate the relative rates of evaporation from the leaves tested in terms of the rate of evaporation from a standard evaporating surface, as of free water, at the same temperature and under the same general conditions.

After preliminary experimentation, it became apparent that a modification of the well known cobalt paper test devised by Stahl⁶ gave promise of meeting the conditions of our problem. It will be remembered that cobalt chloride has the property of appearing blue when dry and red when hydrated. Taking advantage of this fact, Stahl prepared an hygrometric paper which is blue when dry and which alters its color to white or pale rose-color when moist. The paper loses all of its blue color when it has absorbed a certain amount of water, and it can be prepared so as to be very uniform and very sensitive. Stahl's object was to compare the transpiring power of different leaves and of the two surfaces of the same leaf, no attempt being made, however, to standardize these findings to any physical surface. When small pieces of the cobalt paper were appressed to a leaf surface, held in position and protected from the external air by means of glass or mica plates, the time required for loss of blue color was taken as an index of the transpiring power of the leaf in question.

It was early found in the present studies that the paper used must be comparatively thin, in order to give a quick response.

⁶ Stahl, E., Einige Versuche über Transpiration und Assimilation. *Bot. Zeitg.* 52: 117-146, 1894.

It is also desirable that it be opaque, so as not to allow transmitted light from the leaf to confuse the color judgment of the observer. No doubt the quality of the paper most suitable will vary with the properties of the leaves to be studied; as will shortly appear, it is not essential always to make use of the same paper. A thin rough-surfaced writing-paper proved satisfactory, but the best success was obtained with the "tissue towel" paper, now on the American market. It somewhat resembles soft filter paper, but is much thinner. It is very uniform in quality and thickness, is very bibulous and sufficiently opaque.

The paper is saturated with a 3% solution of cobalt chloride and suspended by one edge to dry. The most uniformly colored portions of the sheets are then selected, cut into small squares (about 7 mm. on a side) and these preserved in a suitable stoppered bottle. Each paper slip is dried just before use, by passing it several times over a small flame, as of a candle, the slip being held in a pair of forceps and the position of the forceps being changed during the operation, so as to give a uniform blue color throughout. An acetylene lamp such as is in use for bicycles has proved convenient for drying the papers, as well as for night observations.

The standard of water supplying power first adopted was that of the air at a distance of approximately one millimeter from a free surface of pure water. A small glass vial, with the top ground plane, is filled with water and the excess is carefully removed with absorbent paper, till the margin of the meniscus is definitely below the free edge of the glass. A square of dry cobalt paper is laid over the mouth of the vial, thus coming to lie within about a millimeter of the liquid water, and a plain glass plate is quickly superimposed. Observation is made of the time required for the complete disappearance of blue color. A second vial like the first, over which a square of paper and its glass plate are left continuously, furnishes the eye with a color standard for comparison. The test is repeated, with the same and with other paper slips, and a uniform lot are thus selected. It is found that there is but little variation in the rapidity of response of the various slips at the same temperature. The

paper used in these experiments, placed upon such vials as the one just described, loses its blue color in from 13 to 30 seconds, depending of course on the temperature. Neither the water tests nor the leaf tests may be carried out with direct sunshine falling upon the apparatus. A small shade is sufficient.

Placed against the moist air, which is continually supplied with water vapor from the adjacent water surface, the paper begins immediately to absorb moisture, the rate of this absorption depending upon the rate at which aqueous vapor can reach the paper surface, and upon that at which the moisture is fixed through the hydration of the cobalt salt. The former of these rates should be constant for any arrangement of vial and water surface, and for any given temperature of the water. The latter rate falls continuously as water enters the paper. Finally, when all blue color has disappeared, a certain amount of water has been absorbed, which depends on the quantity of salt held in the paper, the thickness of the latter, etc. It is not requisite, however, to determine this amount, it being a constant which falls away in the calculations. Of course absorption continues after the color change has been produced, since the paper is by no means saturated at the critical point of the indicator, but of this further absorption there is no visible evidence.

The use of the free water surface is attended with several difficulties. To avoid some of these, Mr. E. M. Harvey devised a simple apparatus by which the hygrometric paper can be brought to lie within about a millimeter of the surface of a piece of water-saturated blotting paper.⁷ The wet paper lies beneath a sheet of vulcanite which is perforated by two circular openings about 8 mm. in diameter and about a centimeter apart. A glass plate

⁷ A saturated paper of this sort evaporates water for a long time at the same rate as does an equivalent area of free water surface. On this point see the following: Renner, O., *Zur Physik der Transpiration*. Ber. d. d. Bot. Ges., **29**: 451-547, 1911. Reviewed in *Plant World* **14**: 195-196, 1911.

Livingston, B. E. and Brown, W. H., Relation of the daily march of transpiration to variations in the water content of foliage leaves. *Bot. Gaz.* **53**: 309-330, 1912.

The paper in Mr. Harvey's apparatus is kept constantly saturated by dipping below into a small reservoir of water.

lies over the vulcanite and is provided with a paper screen on its upper surface. This screen is perforated with two circular windows corresponding to the openings in the vulcanite below. On the lower side of the glass plate, under one of the windows, is gummed by its margin a piece of the cobalt chloride paper large enough to cover completely one of the windows. This gives the standard color of the hydrated paper. The test paper is quickly inserted over the remaining opening (under the second window) the glass is returned to place, and observation is made of the time required for the test paper to become of the same color as the standard. Tests are more readily carried out with this apparatus than with the vials.

For applying the paper slips to the plant leaves, small spring clips are used, formed of hard brass wire, to either arm of which is cemented—by means of De Khotinsky cement—a small glass plate. The glass plates used in the present work were cut cross-wise from ordinary microscopic slides and are about 12 mm. wide and 21.5 mm. long. About a third of its outer surface is occupied, at one end of each plate, by the cement attachment of the corresponding arm of the wire part. The two inner faces of the plates lie in contact when the clip is closed, its position of rest, and pressure upon the looped portion of the wire separates the plates, keeping their surfaces nearly parallel. The general form of the wire is not unlike that of an ordinary pinch-cock for rubber tubing, the wire loop being the handle in the present case. The cobalt paper slips should be small enough so as not to reach to the edges of the glass plates when held between them.

It is expeditious, after drying a paper, to insert it between the plates of a clip, and so bring it to the leaf to be tested. If the leaf be held horizontally, the clip may now be opened so that the paper rests on the lower plate, and the clip may then be moved forward till the leaf lies over the paper and between the plates. On closing the clip the paper is brought into the desired position on the under side of the leaf. A very little practice leads to facility in these operations. Only a single paper should usually be applied with one clip. To place a paper on the normally upper side of a leaf, the latter may be turned till this surface comes to

lie below, or the paper may be laid upon the leaf surface, after which the clip may be placed. The clips are sufficiently light so that they may be left hanging on the leaves of most plants during the interval of the test, but it is a simple matter to arrange supports for them.

A paper having been placed upon a leaf, the time required for complete loss of blue color is carefully noted. It is well to facilitate the determination of the endpoint by having previously prepared a clip with a piece of leaf of the kind to be tested, held between two squares of hygrometric paper. Thus are provided color standards for both upper and lower foliar surfaces, and the bit of paper has, in each case, a margin or background of the same nature as have those in the actual tests. Several parallel and simultaneous tests are made and the results obtained are averaged for each leaf surface. The results obtained from the two leaf surfaces are averaged to give the index for the surface of the leaf as a whole.

The water test must be made under the same temperature conditions as the leaf tests, it being assured that the water of the standard surface has been allowed time to assume the general air temperature. Between tests, the standard surface should be kept covered, to prevent evaporation with its consequent cooling. A stop watch is almost essential for the water test and is convenient for the leaf tests.

To illustrate the manner of manipulating the results an example may be given. Let it be assumed that the water test gives an average time period of 15 seconds and that the corresponding average for the lower leaf surface of a certain plant is 300 seconds, while that for a second plant is 600 seconds. It is clear that the water-supplying power of the lower foliar surface of the first plant is $15/300$, or 0.05 of that of the air that lies against the paper in the water test, while the lower surface of the leaves of the second plant can give off water only one-half as rapidly, their transpiring power being 0.025 of that of the standard surface. These transpiring powers should be approximately the same as the relative transpiration ratios derived indirectly. The indices of transpirational retardation are, in the above example, 20 and

40, respectively, referred to the air-paper surface of the water test. They are directly proportional to the cobalt paper times.

It is obvious that all of the leaves of a plant cannot usually be subjected to the paper test, but the commonly used method of random sampling may here be resorted to. A sufficient number of tests may be carried out to give to the resulting average an adequate accuracy. Of course it is impracticable to obtain indices by this procedure, from surfaces which are covered by a water film or which bear water droplets, as occurs with the fall of rain or the formation of dew. Under such conditions, however, absolute transpiration must approach zero or become actually negative through slight foliar absorption. This is a consideration which makes it seem unnecessary to attempt the measurement of the internal resistance to transpiration at such times. Hairy leaves and those which are much wrinkled or folded introduce difficulties also, since with such surfaces the effect of the external air upon the hygrometric paper is not readily excluded.

When the transpiring power of a surface is very low, the time required for complete disappearance of blue color in the test paper may be shortened by using a thinner paper, or it is possible to adopt a color standard from which all of the blue color has not disappeared and to bring all test papers to this color rather than to the complete response. Furthermore, the error in the observed time of response, due to the momentary exposure of the dried paper to the air, may assume considerable importance in a very humid atmosphere. Nevertheless, the procedure above described has been followed successfully at all hours of the day and night, in a greenhouse, under the climatic conditions of a rainy summer in Munich.

The details of the application of the cobalt chloride method to the more difficultly manipulated plant surfaces and of its employment under otherwise adverse conditions, remain mainly to be elaborated. Under most circumstances, however, the method above described is very simple of operation and requires no complicated or expensive apparatus. It is well suited to operations in the field, furnishing a ready means for the comparison of upper and lower, or younger and older, leaves of the same plant, or of

the same leaf at different stages of its development, in respect to the resistance offered to transpiration. Also, we have here a method which should be very valuable in comparing the transpirational retardation of the foliage of different plant forms, whether growing in the same or in remote localities, a line of investigation which has not heretofore been attempted and which should do much to advance both ecology and agriculture. As far as resistance to transpiration is concerned, it would seem that we might now be able to give something of a much needed quantitative turn to the description and classification of ecological forms.

The only cases so far met with in which the method just described fails utterly are those of extremely xerophytic leaves, upon which the hygrometric paper does not completely lose its blue color. Such is true, for example, of the upper surface of the older leaves of the tree tobacco, *Nicotiana glauca* Graham. Here we have apparently to deal with a question, not of rate at all, but of vapor pressure. It seems that the leaf surface in such cases possesses a lower vapor pressure than does the hygrometric paper at its critical point of color change. This whole matter still awaits investigation.

EXPERIMENTATION

Although the method of standardized cobalt chloride paper may be applied to other plant surfaces, the experimental data to be presented in this section deal with foliage leaves only; foliar transpiration is generally by far the most important form of water loss, and it has seemed best, in the beginning of studies of this kind, to confine attention to foliar conditions. The following experiments have been selected from a larger number, the aim of this presentation being to bring out some of the uses of the standardized paper method, on the one hand, and to indicate, on the other, some of the possible variations in foliar resistance to transpiration.

The potted plants for these studies were grown without shelter, in sheet metal cylinders, and, while not as large as others of similar age in the open soil, they showed no evidence of being otherwise unusual.

In the presentation below, all of the original data will not be given, selected samples being allowed to indicate the methods of manipulation and calculation to which the original observations have been subjected.

Experiment I. This series of observations brings out the absolute values and the range of variation in transpirational retardation for a single species under the conditions of the experiment, and also makes possible a direct comparison of results obtained by means of the method of cobalt chloride paper with other results derived through the relative transpiration ratio. The series was carried out with potted plants *Physalis angulata* L. var. *linkiana* Gray, a plant that occurs plentifully in the experiment grounds of the Desert Laboratory, developing vigorously and producing flowers and fruit in the season of the summer rains. The experiment continued from 21 hours of July 25 to 12 hours of the following day. At 11 hours 35 minutes, the series was interrupted by a heavy shower, which necessitated the removal of the plants and instruments into the laboratory.

Two observations with cobalt chloride paper were made hourly, for the upper and for the lower leaf surface, the water test (with free water surface) being also made. Two plants were used, the tests being made with leaves of medium age. Different leaves were employed for consecutive hours. The plants were taken into the laboratory for the paper test and returned to the open as soon as this was completed.

Hourly readings of a white atmometer and of a brown radio-atmometer,^a—both instruments drawing water from burettes,—were obtained, also hourly weighings of two sealed potted plants, and the relative transpiration ratios were derived according to the methods described in Publication 50 of the Carnegie Institution. The atmometers were both placed in the inclined position, to make the angle of incidence of the sun's rays upon the cup approximately constant throughout the day. The instruments remained in the open until 11 hours 30 minutes, the plants were taken into

^a Livingston, B. E., A radio-atmometer for measuring light intensities. *Plant World*, 14: 96-99, 1911.

Idem. Light intensity and transpiration. *Bot. Gaz.*, 52: 418-438, 1911.

the laboratory for a few minutes at each weighing. The different operations were always carried out in the same order, and there occurs in this series but little discrepancy between the actual time at which any observation was taken and that which would have been requisite to give an hourly rate. The errors produced by slight variations in the length of the time periods have been ignored in this experiment.

Table 1 presents samples of the original data from the paper tests, for hours 21 and 7, and also shows the manner of manipulating these data in the derivation of the indices of transpiring power for the two leaf surfaces and for the leaf as a whole.

TABLE 1

		HOUR NO.	
		21	7
Time required for paper response, seconds:			
Over water.....		13	18
Upper leaf surface	{ Test 1.....	600	480
	{ Test 2.....	840	420
	{ Average.....	720	450
Lower leaf surface	{ Test 1.....	2100	300
	{ Test 2.....	3000	300
	{ Average.....	2550	300
Index of transpiring power, ratio of water test time to average leaf time:			
Upper leaf surface.....		0.018	0.040
Lower leaf surface.....		0.005	0.060
Average index for whole leaf.....		0.012	0.050

In table 2 (columns 2, 5 and 8) are given the indices of transpiring power for the two leaf surfaces, and the average indices for the entire leaf surface, for each observation. To obtain the average indices of transpiring power for each hour period, the indices from each two consecutive observations have been averaged, and the averages thus derived are also included in this table (columns 3, 6 and 9). Furthermore, the values of the last-named indices after reduction to a uniform basis for comparison (the index for hour 1), are likewise included (columns 4, 7 and 10).

It is evident at once from table 2 that the index of transpiring power varies definitely with the different hours of the day, and

that this is true for both leaf surfaces and for their averages, which represent the whole leaf. While the indices were 0.018 for the upper and 0.005 for the lower leaf surface at the end of hour 21, the former index increases to 0.081 at the end of hour 8 and the latter to 0.120 at the end of hour 12. The index of the leaf as a whole, on the basis of the actual times of observation, varies from 0.0115 (hour 21) to 0.0960 (hour 12). The order of

TABLE 2

HOUR	INDEX OF TRANSPIRING POWER, PHYTALIS								
	UPPER LEAF SURFACE			LOWER LEAF SURFACE			ENTIRE LEAF SURFACE		
	At end of hour	For preceding hour		At end of hour	For preceding hour		At end of hour	For preceding hour	
		Actual	Relative to hour 1		Actual	Relative to hour 1		Actual	Relative to hour 1
(July 25)									
21	0.018			0.005			0.0115		
22	0.021	0.0195	0.89	0.012	0.0085	0.65	0.0165	0.0140	0.80
23	0.024	0.0225	1.02	0.009	0.0105	0.81	0.0165	0.0165	0.94
24	0.023	0.0235	1.07	0.015	0.0120	0.92	0.0190	0.0178	1.02
(July 26)									
1	0.021	0.0220	1.00	0.011	0.0130	1.00	0.0160	0.0175	1.00
2	0.023	0.0220	1.00	0.018	0.0145	1.12	0.0205	0.0182	1.04
3	0.035	0.0290	1.32	0.020	0.0190	1.46	0.0275	0.0240	1.37
4	0.025	0.0300	1.36	0.025	0.0225	1.73	0.0250	0.0263	1.55
5	0.025	0.0250	1.14	0.063	0.0440	3.38	0.0440	0.0345	1.97
6	0.036	0.0305	1.39	0.070	0.0665	5.11	0.0530	0.0485	2.77
7	0.040	0.0380	1.73	0.060	0.0650	5.00	0.0500	0.0515	2.94
8	0.081	0.0605	2.75	0.089	0.0745	5.73	0.0850	0.0675	3.86
9	0.067	0.0740	3.36	0.078	0.0835	6.42	0.0725	0.0788	4.50
10	0.062	0.0645	2.96	0.087	0.0825	6.34	0.0745	0.0735	4.20
11	0.072	0.0670	3.05	0.103	0.0950	7.31	0.0875	0.0810	4.63
12	0.072	0.0720	3.27	0.120	0.1115	8.58	0.0960	0.0918	5.24

occurrence of the variations will be considered later, as will also the range of the average condition for the hour period; attention is best confined here to the degree of variation and its meaning. It will be recalled that the index under consideration is, in each case, the quotient obtained by dividing the time necessary for the paper response in the water test by the corresponding time required for this response on the leaf surface. Since the cobalt

chloride paper gives its color response when a certain definite amount of moisture has been absorbed, and since the moisture absorbed in the leaf tests must necessarily emanate from the leaf, it follows that we have, in the indices here presented, approximate measures of the possible rates of water exit from the leaves, these measures being stated in terms of the possible rate of evaporation, under the same conditions, from a water surface covered by a millimeter of vapor and air blanket. Thus, when the index of transpiring power of the lower leaf surface of our plant is 0.096, this means simply that, at the end of hour 12, 1000 area units of the leaf surface in question could supply moisture to any set of aerial surroundings at the same rate as would 96 area units of a free water surface blanketed by a millimeter layer of air.

It is to be noted that the range of transpiring power is very much greater for the lower than for the upper leaf surface; for the former the range is from 0.005 to 0.120 or from unity to 24.0, and for the latter it is from 0.018 to 0.081 or from unity to 4.5. Furthermore, it is interesting to observe that the greater range of variation of transpiring power exhibited by the lower leaf surface is not entirely due to a higher maximum than that attained by the upper surface, but also to a markedly lower minimum. At the time of greatest retardation of water loss on both sides of the leaf, the transpiring power of the upper surface is still 3.6 times as great as that of the lower. A discussion of the causes of these differences would be premature at present and out of place in this paper.

Table 3 presents the data of transpiration from the two plants, those of evaporation for the two atmometers, and the relative transpiration ratios derived for each plant as compared to each instrument. Each series of data has been reduced to a comparable series, with the datum for hour 1 as unity. That the actual losses from which the reduced rates have been obtained may readily be reverted to, the actual value for hour 1 is inserted in the table, in parentheses, below the item 1.00 (for hour 1) in each series. Thus it is possible to obtain the actual observed rate from plant or instrument, for any given hour. The inserted atmometric

data have been corrected to the Livingston standard for this instrument.⁹

In table 3 the ratio of relative transpiration by the white atmometer, which absorbs comparatively little heat from the sunshine, varies from 0.91 to 6.11 (1.0 to 6.7) and from 1.00 to 5.88, for the two plants, respectively. By the brown instrument, which sums the effect of sunshine together with that of the evaporating power of the air, these variations are from 0.89 to 5.66 (1.0 to 6.4)

TABLE 3

HOUR	TRANSPIRATION, <i>PHYSALIS</i>						EVAPORATION	
	ABSOLUTE		RELATIVE				White atmometer	Brown atmometer
	Plant 1	Plant 2	Plant 1		Plant 2			
			By white atmometer	By brown atmometer	By white atmometer	By brown atmometer		
22	1.11	1.47	0.91	0.89	1.20	1.18	1.22	1.25
23	1.11	0.94	1.66	1.82	1.40	1.54	0.67	0.61
24	1.03	1.15	1.07	1.06	1.20	1.19	0.96	0.97
1	1.00 (0.35)	1.00 (0.34)	1.00	1.00	1.00	1.00	1.00 (2.03)	1.00 (2.09)
2	1.25	1.24	1.47	1.51	1.46	1.49	0.85	0.83
3	1.03	1.85	2.15	2.64	1.77	2.18	0.48	0.39
4	0.78	1.03	3.54	3.12	4.68	4.12	0.22	0.25
5	0.97	1.12	2.62	2.94	3.03	3.39	0.37	0.33
6	2.97	3.59	3.81	2.88	4.60	3.49	0.78	1.03
7	5.83	7.14	3.94	3.04	4.82	3.72	1.48	1.92
8	7.03	6.76	6.11	4.95	5.88	4.76	1.15	1.42
9	8.39	8.79	5.38	4.37	5.64	4.58	1.56	1.92
10	8.61	8.29	4.39	3.60	4.23	3.47	1.96	2.39
11	11.88	10.59	4.72	4.03	4.21	3.59	2.52	2.95
12	5.66	3.06	5.44	5.66	2.94	3.06	1.04	1.00

and from 1.00 to 4.76. The average range of the ratio, by the white atmometer, for the two plants, is 1.0 to 6.3, and the average range of the ratio by the brown instrument is 1.0 to 5.6. It is to be remembered that these ratios represent average conditions for the hour, and, consequently, to compare the ranges just given with those of the index obtained from the paper test, it is necessary to use for the latter likewise, the range of the average con-

⁹ Livingston, B. E., Operation of the porous cup atmometer. *Plant World* 13: 111-118, 1910.

dition for the hour. From table 2 it is found that this range is 0.80 to 5.24, or 1.0 to 6.6. The different values obtained for the range of transpiring power in the plants of experiment I, may be summarized as follows:

Range of relative transpiration ratio for Physalis

By white atmometer

Plant 1.....	1 to 6.7
Plant 2.....	1 to 5.9
Average.....	1 to 6.3

By brown atmometer

Plant 1.....	1 to 6.4
Plant 2.....	1 to 4.8
Average.....	1 to 5.6

Range of index of transpiring power

By paper test.....	1 to 6.6
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It is evident that the result arrived at by means of the cobalt chloride paper is in very satisfactory agreement with those derived by the indirect methods.

To compare the different series, in regard to the manner of occurrence of the variations which they indicate, graphs have been prepared for each series. The two graphs of relative transpiration for one plant are so nearly identical with those for the other, that the graphs for plant 1 alone are given here.

Figure 1 presents the graphs of the relative transpiration of plant 1, by the white and by the brown instrument, the graph of the transpiring power of the leaves as a whole (by hygrometric paper), that of absolute transpiration of plant 1 and that of evaporation from each of the two atmometers. All of the graphs are comparable throughout, being constructed to pass through a common point at hour 1. The abscissae represent hourly intervals and the ordinates are taken directly from tables 1 and 2. Dawn occurred this day at about 3 hours 30 minutes, sunrise at 6 hours. The forenoon was partly cloudy, as is clearly shown by the behavior of the atmometers. There was very little wind

at any time, excepting for a few minutes about 11 hours 25 minutes, when the approach of the storm already mentioned was accompanied by several strong gusts. With the coming of rain, at 11 hours 35 minutes, the instruments and plants were taken into the laboratory.

The general agreement of the three graphs bearing upon transpiring power is such that if all three were smoothed so as to eliminate irregularities in the lines, all would be in very satisfactory agreement. As should be expected, the relative transpiration graph by the white atmometer is uniformly higher than that by the brown instrument during the hours of sunshine, the absorption of radiant energy causing the rate of water loss from the brown cup to exceed the rate from the white one. Since sunshine must always accelerate transpiration, because of the absorption of some radiant energy by the leaves, the brown instrument is theoretically better suited to the determination of transpiring power and its variations than is the white,¹⁰ and in this connection it is clear that the graph from the dark instrument is more nearly in agreement with that from the paper test than is the other. That the relative transpiration graphs exhibit marked accelerations and retardations that are only slightly, or not at all, indicated by the graph from the direct method seems to be explained by the supposition that the atmometers are much more sensitive to changes in the surrounding conditions than are the plants. There is available, from other sources, much evidence in favor of this supposition, but the time for detailed discussions of these minor questions has not yet arrived.

Experiment II. This is a series of observations similar to that of experiment I, carried out with the same purposes in view. The plants used were small specimens of *Datura stramonium* L. Two series of hourly weighings, for the absolute transpiration rates, were carried out, also the white atmometer and the brown radio-atmometer were operated with hourly readings. The cobalt chloride test was applied hourly to the upper and lower surfaces of leaves of medium age, four plants being used, two at each deter-

¹⁰ Livingston, B. E. Light intensity and transpiration. *Loc. cit.*

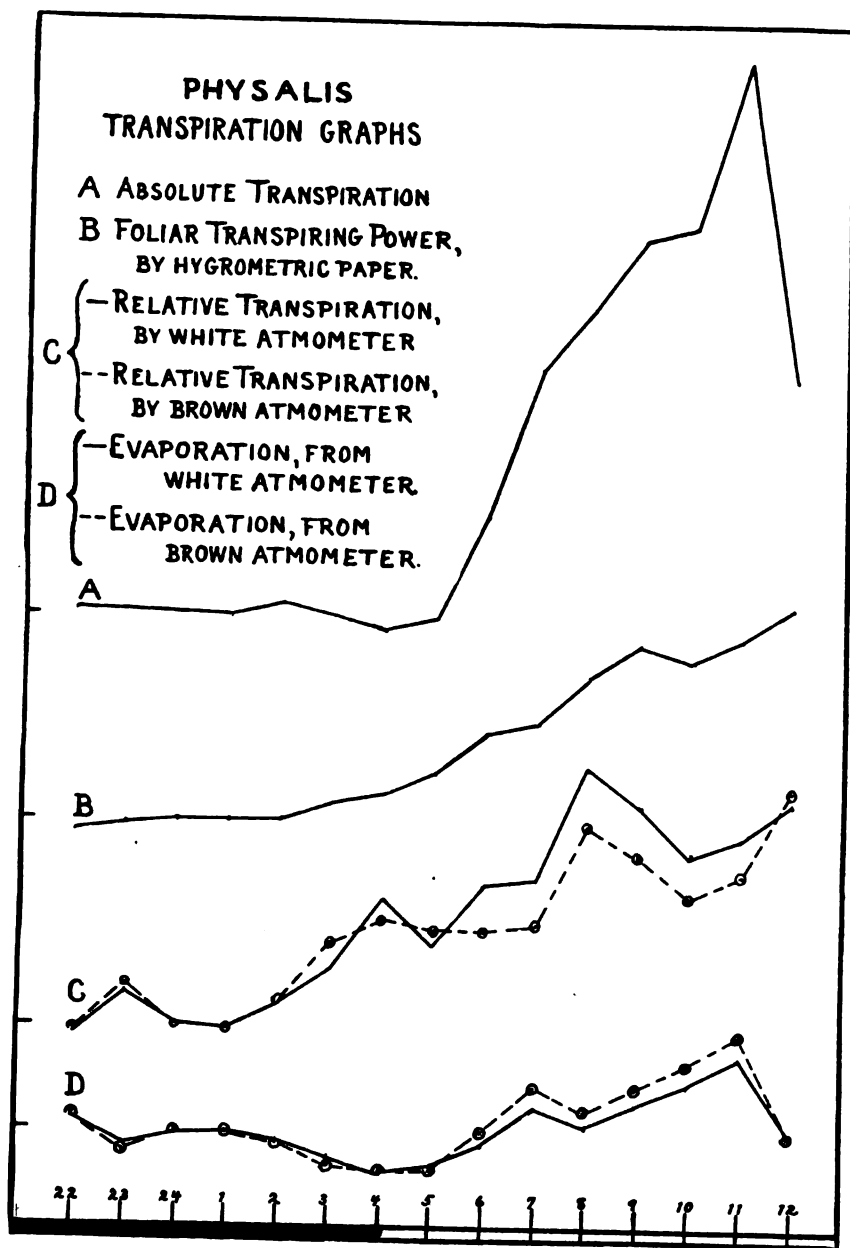


Fig. 1

mination. No two consecutive determinations were made upon the same plant. From four to eight tests were made in each case, the results being averaged for each of the two leaf surfaces. The water test was carried out hourly, in a similar way, and the results averaged. The time required for the color response of the hygrometric paper over the standard water surface varied from 18 sec. (hours 11 to 13) to 27 seconds (hours 1 to 4). The experiment began at 11 hours, September 2, 1911, and ended at 14 hours, the day following. The day was almost entirely clear, with very few light clouds. Dawn occurred about 4 hours and sunrise about 5 hours.

Table 4 presents the indices of transpiring power for the upper and lower foliar surfaces, for the end of each indicated hour, as well as for the hour period preceding, these indices being derived quite as in experiment I. The table also includes the averages of the upper and lower indices for the hour periods, these averages being taken to represent the condition of the entire leaf surface as to its transpiring power. They are, therefore, more or less comparable to the corresponding relative transpiration ratios. The three different series are also given in the reduced form, the reduction being so made in this instance as to relate each index to the lowest one of the series as unity. It will be noticed that this method does not necessarily bring unity in the reduced series to the same hour, as does the method resorted to in experiment I. The numbers have all been rounded off with the third place of decimals for the primary series and with the first place for the final reduced series in each case. The rounding off was not performed, however, until after the various necessary operations had been accomplished; the accuracy of our figures is far greater than is requisite in such studies as this. The data for the entire leaf surface at the ends of the hours have been omitted from this table; they are readily to be obtained by averaging the corresponding numbers in columns 2 and 5. The items of column 8 have been derived by averaging the corresponding ones of column 3 and 6.

In general character, the data of table 4 agree with those of table 2. Here, as in the former experiment, the range of tran-

TABLE 4

HOUR	INDEX OF TRANSPIRING POWER, DATURA							
	UPPER LEAF SURFACE				LOWER LEAF SURFACE			
	At end of hour	For preceding hour		At end of hour	Actual	For preceding hour		ENTIRE LEAF SURFACE FOR PRECEDING HOUR
		Actual	Relative to hour 22			Actual	Relative to hour 24	
(September 2)								
11	0.298			0.219				
12	0.284	0.291	11.2	0.460	0.340	21.9	0.315	14.8
13	0.287	0.286	11.0	0.429	0.445	28.7	0.365	17.1
14	0.252	0.270	10.4	0.440	0.435	28.0	0.352	16.5
15	0.338	0.295	11.4	0.466	0.453	29.2	0.374	17.6
16	0.233	0.286	11.0	0.415	0.441	28.4	0.363	17.0
17	0.186	0.210	8.1	0.295	0.355	22.9	0.282	13.2
18	0.097	0.142	5.4	0.140	0.218	14.0	0.180	8.4
19	0.050	0.074	2.8	0.065	0.103	6.6	0.088	4.1
20	0.026	0.038	1.5	0.022	0.044	2.8	0.041	1.9
21	0.026	0.026	1.0	0.031	0.027	1.7	0.026	1.2
22	0.026	0.026	1.0	0.021	0.026	1.7	0.026	1.2
23	0.027	0.027	1.0	0.017	0.019	1.2	0.023	1.1
24	0.027	0.027	1.0	0.014	0.016	1.0	0.021	1.0
(September 3)								
1	0.030	0.029	1.1	0.017	0.016	1.0	0.022	1.0
2	0.029	0.030	1.1	0.017	0.017	1.1	0.023	1.1
3	0.033	0.031	1.2	0.024	0.021	1.3	0.026	1.2
4	0.038	0.036	1.4	0.040	0.032	2.1	0.034	1.6
5	0.102	0.070	2.7	0.124	0.085	5.5	0.078	3.6
6	0.118	0.110	4.7	0.145	0.135	8.7	0.122	5.7
7	0.143	0.131	5.6	0.178	0.162	10.4	0.146	6.9
8	0.143	0.143	6.0	0.159	0.169	10.9	0.156	7.3
9	0.152	0.147	6.0	0.171	0.165	10.7	0.156	7.3
10	0.200	0.176	7.1	0.212	0.192	12.4	0.184	8.6
11	0.222	0.211	7.5	0.353	0.283	18.2	0.247	11.6
12	0.243	0.253	10.3	0.413	0.383	18.3	0.268	12.5
13	0.293	0.268	10.3	0.394	0.404	26.0	0.336	15.8
14	0.240	0.267	10.2	0.369	0.382	24.6	0.324	15.2

spiring power indicated by our indices is very much greater for the lower than for the upper leaf surface; for the former the range is from 0.014 (24 hours) to 0.466 (15 hours), or from unity to 33.1; for the latter surface it is from 0.026 (24 to 22 hours) to 0.298 (11 hours), or from unity to 11.5. It is again apparent that the minimum index for the lower surface (0.014) is much

lower than that of the upper (0.026). When water loss is most retarded in both cases, the transpiring power of the upper foliar surface of *Datura* is about 1.9 times as great as that of the lower. This point may be emphasized in another way by noting that, from 22 hours of the first day to 3 hours of the second, the transpiring power of the upper leaf surface exceeds that of the lower surface in actual magnitude, while the converse holds for the daylight hours. The diurnal march of the indices will be considered below.

In table 5 are given the ratios of relative transpiration, derived from the absolute losses of the two plants of *Datura* and from those of the two atmometers. The average ratios with reference to each instrument are also given. All have been reduced to a basis of the datum of hour 8 as unity, this datum representing the lowest value in each series. Since there was considerable variation in the actual time periods of this experiment, all losses were first computed to hourly rates for hourly periods, and it is from these corrected rates that the data of the table have been derived.

The ranges of variation of the ratios of relative transpiration, as given in table 5, are to be compared with the range of variation of the indices of transpiring power derived from the hygrometric tests. This comparison may best be accomplished by the following summary:

Range of ratio of relative transpiration for Datura

By white atmometer

Plant 1.....	1 to 11.5
Plant 2.....	1 to 18.7
Average.....	1 to 14.1

By brown atmometer

Plant 1.....	1 to 9.2
Plant 2.....	1 to 15.8
Average.....	1 to 12.5

Range of index of transpiring power

By hygrometric test.....	1 to 17.6
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It becomes at once clear that the ranges of the ratios of relative transpiration for plant 2 are in satisfactory agreement with that of the index. The latter range is about 6 per cent smaller than that of the relative transpiration ratio by the white instrument, and about 11 per cent greater than that of the ratio by the brown

TABLE 5

HOUR	RATIOS OF RELATIVE TRANSPIRATION, DATURA					
	BY WHITE ATMOMETER			BY BROWN ATMOMETER		
	Datura 1	Datura 2	Average	Datura 1	Datura 2	Average
(September 2)						
13	9.4	18.7	14.1	7.8	15.7	11.8
14	8.3	15.4	11.9	6.8	12.8	9.8
15	10.1	17.2	13.7	9.2	15.8	12.5
16	7.3	10.8	9.1	6.4	9.6	8.0
17	7.2	9.0	8.1	6.5	8.1	7.3
18	3.6	5.0	4.3	3.5	4.9	4.2
19	1.7	2.1	1.9	1.7	2.2	2.0
20	1.0	1.0	1.0	1.0	1.0	1.0
21	2.1	2.2	2.2	2.3	2.5	2.4
22	2.6	3.0	2.8	2.9	3.3	3.1
23	2.2	3.0	2.6	2.0	2.9	2.5
24	1.5	2.2	1.9	1.6	2.4	2.0
(September 3)						
1	3.0	3.2	3.1	3.2	3.3	3.3
2	5.0	4.0	4.5	4.5	3.7	4.1
3	2.6	2.4	2.5	2.4	2.2	2.3
4	4.8	6.4	5.6	2.3	3.1	2.7
5	4.9	4.0	4.5	4.5	3.6	4.1
6	5.7	7.2	6.5	8.5	10.8	9.7
7	9.1	11.3	10.2	6.5	8.2	7.4
8	9.6	8.0	8.8	7.0	5.8	6.4
9	10.4	8.0	9.2	8.2	6.4	7.3
10	11.3	11.1	11.2	9.0	9.0	9.0
11	10.0	6.0	8.0	8.4	5.2	6.8
12	11.5	5.0	8.3	9.1	4.0	6.6
13	11.2	4.8	8.0	9.1	4.0	6.6
14	9.4	4.0	6.7	7.8	3.4	5.6

instrument. For the other plant the ranges are not in satisfactory agreement, a state of affairs which is of course transmitted to the averages for the two plants. It must be borne in mind that the same plants were not used for the cobalt chloride tests and for the transpiration determinations, and that it is possible that

special conditions may have been operative on one plant and not upon another.

Figure 2 presents the graphs for the three series of indices (table 4, column 4, 7 and 9) and for the two series of average relative transpiration ratios (table 5, columns 4 and 7). Figure 3 repeats the graph representing the indices for the entire leaf surface, and also shows the graphs for the four series of relative transpiration ratios for the individual plants.

Inspection of the graphs brings out the fact that there is a much greater uniformity and consistency in the march of the index of transpiring power derived from the standardized hygrometric paper than is found in the march of the ratio of relative transpiration. While the minor irregularities in the ratio graphs may safely be related to non-uniformities in the fluctuation of the surrounding conditions of the weighed plants and of the instruments, the more pronounced discrepancies between the results of the two methods with which we are dealing must have some other explanation. Perhaps the most striking of these greater discrepancies lies in the fact that, while the index remains low and almost constant throughout the night hours, the ratio shows an unmistakable tendency to increase in value after the early attainment of its minimum. No explanation of this condition can now be offered.

Another striking discrepancy between the graphs of the ratio, on the one hand, and of the index, on the other, manifests itself in the early fall of the values of the ratio in the case of plant 2. This appears probably to be related to incipient drying,¹¹ which may have occurred in plant 2 while it had not yet been sensibly induced either in plant 1 or in the plants used in the hygrometric tests.

It is also remarkable that the relative transpiration ratio of plant 1, by either atmometer, presents a much flatter graph than that exhibited by the hygrometric index of transpiring power.

In spite of discrepancies, however, the conclusion is forced upon us that the results obtained by means of the two methods are

¹¹ Livingston and Brown. *Loc. cit.*

Livingston, B. E., Incipient drying in plants. *Science N. S.*, **35**: 394-395, 1912.

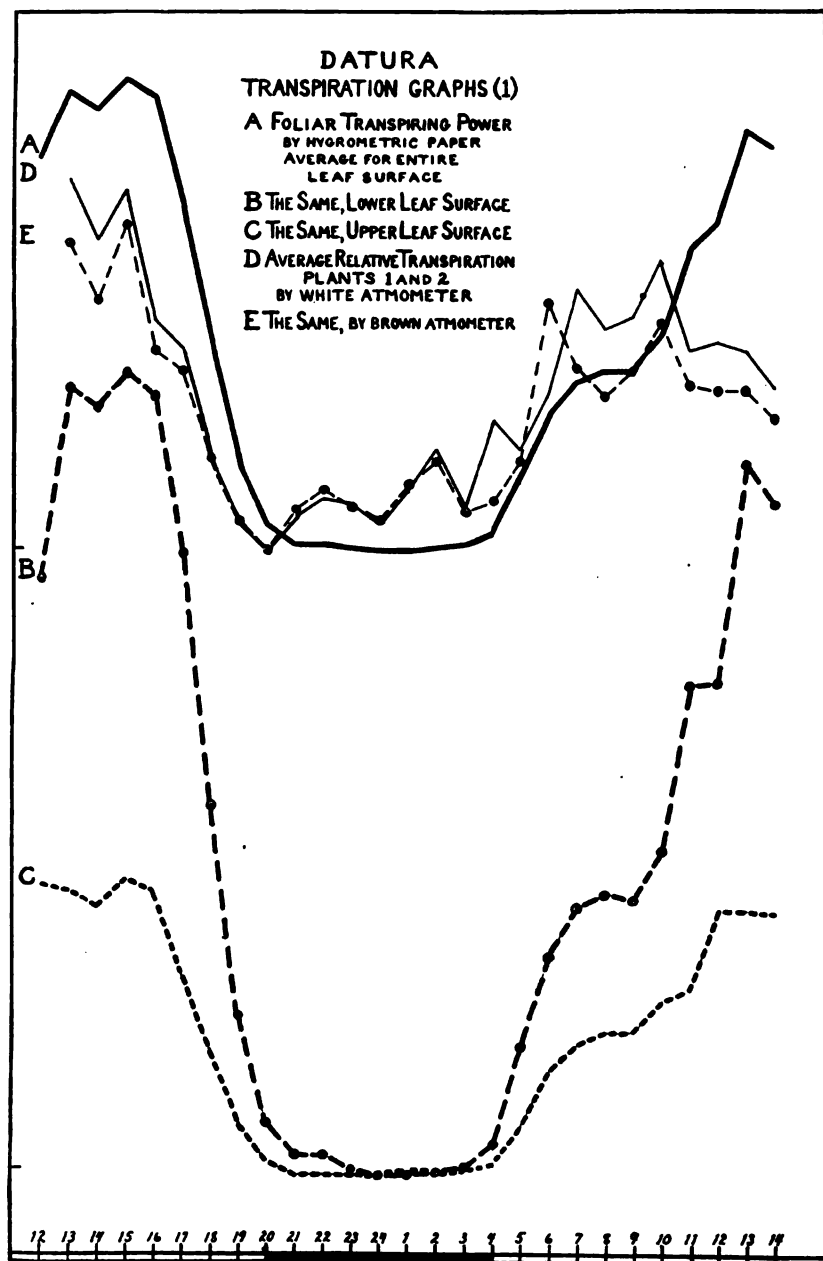


Fig. 2

much more in agreement than they are in disagreement, and the student of such series of observations as have been presented above finds himself unable logically to ascribe greater reliability to either of the two methods. Of course neither is to be considered as quantitatively accurate, yet in the present state of our knowledge of the dynamics of plant transpiration, it is clear that both methods promise to be of great value for the future development of physiology and physiological ecology.

Experiment III. In this experiment is considered merely the comparison of the indices of transpiring power for two widely different forms at the same time. At 10 hours 30 minutes September 17, 1911, potted plants of *Zea mais* L. (about 40 cm. in height) and of *Martynia louisiana* Mill. (about 6 leaves each), which had been grown in the open at the Desert Laboratory, were subjected to the cobalt chloride test. The average time periods required for the color change (4 to 6 tests in each case) are summarized below, together with the indices of transpiring power derived therefrom.

	LEAF SURFACE	TIME	INDEX
		<i>seconds</i>	
<i>Martynia</i>	upper	40	0.68
	lower	36	0.76
	entire		0.72 (average)
<i>Zea</i>	upper	430	0.064
	lower	446	0.061
	entire		0.063 (average)
Water test.....	(free surface)	27	

It thus appears that in both plants the transpiring powers of the two foliar surfaces are about the same, but that the index for *Martynia* is over ten times that for *Zea*. It is also worthy of note that, according to these figures, the transpiring power of *Martynia* leaves should be about 72 per cent as great as the water-supplying power of our standard water surface.

Experiment IV. These tests bring out the difference between the indices for different leaves of the same plant, at the same time. Potted plants of *Phaseolus vulgaris* L. (the Mexican bean) were

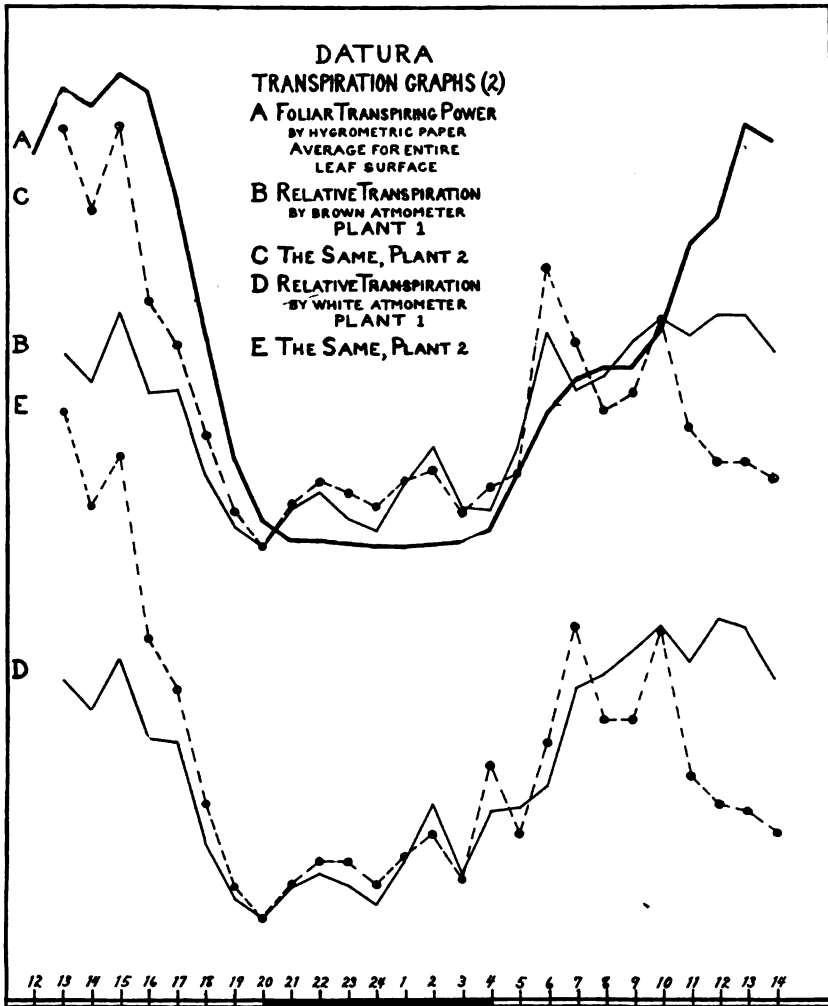


Fig. 3

used, each of which had a pair of very large primary leaves and two or three leaves of the secondary form. It will be recalled that the primary leaves of this plant are simple and that the others have three leaflets. The average test times (for four tests in each case), at 16 hours 30 minutes, September 9, 1911, are given below, as well as the derived indices of transpiring power.

Phaseolus vulgaris

	LEAF SURFACE	TIME	INDEX
		<i>seconds</i>	
Large primary leaves ... {	upper	965	0.031
	lower	278	0.108
	entire		0.070 (average)
Smaller secondary leaves {	upper	570	0.053
	lower	268	0.112
	entire		0.083 (average)
Water test.....	(free surface)	30	

The lower surfaces of the two sorts of leaves have about the same index, but the upper surface of the younger form is apparently characterized by a transpiring power about 70 per cent greater than that of the same surface of the primary leaves. It is also to be noted that the difference between the indices for the two leaf surfaces is greater in the case of the primary leaves than in the others.

Experiment V. This and the experiments to follow were performed in the early autumn of 1912, with the assistance of Mr. E. M. Harvey. The saturated paper standard was used. Experiment V illustrates the differences in transpiring power, between upper and lower leaf surfaces by day and night, for plants of *Ruellia tuberosa* var. *occidentalis* A. Gray, growing in the open ground near the Desert Laboratory, but partially shaded by *Acacia* and *Prosopis*. The plants were rather mature at the time of testing (September 12, 1912), having practically ceased flowering. The tests represent hours 16 and 23.

The results are summarized on following page.

Ruellia tuberosa var. *occidentalis*

		TIME	INDEX
		<i>seconds</i>	
Hour 16.	upper leaf surface	949	0.020
	lower leaf surface	145	0.124
	water test, saturated paper	18	
Hour 23.	upper leaf surface	958	0.038
	lower leaf surface	1101	0.033
	water test, saturated paper	36	

While the index of transpiring power at the daylight observation is about six times as great for the lower leaf surface as for the upper, the two leaf surfaces exhibit practically no difference in transpiring power at the time of the night observation. At the same time it is to be noted that this alteration is not entirely produced by change in the lower surface; the upper surface reveals a much higher index at night than in the day. The average index, representing the entire leaf surface, has a magnitude about twice as great for the daylight observation as for that in the night.

Experiment VI. A flowering plant of *Nicotiana trigonophylla* Dunal., in the open ground and unshaded, near the streamway of the Cañada del Oro, north of Tucson, was tested during the 12th hour, September 1, 1912. The summary of results is given below.

Nicotiana trigonophylla

LEAF SURFACE	TIME	INDEX
	<i>seconds</i>	
Upper.....	270	0.052
Lower.....	149	0.094
Entire.....		0.073 (average)
Water test (saturated paper)	14	

In this case the upper leaf surface appears capable of supplying water to the surroundings at a rate only about one-half as great as that for the lower surface.

Experiment VII. Leaves of the grass *Andropogon halapense* Brot. (Johnson grass) were tested during the fourth hour, August 31, 1912. The plant was growing in the experimental grounds of the Desert Laboratory. The results follow.

Andropogon halapense

LEAF SURFACE	TIME	INDEX
	<i>seconds</i>	
Upper.....	234	0.043
Lower.....	33	0.303
Entire.....		0.173 (average)
Water test (saturated paper).....	10	

Here the index for the lower foliar surface is nearly eight times as great as for the upper.

Experiment VIII. In the open oak forest above Oracle (about 64 kilometers or 40 miles northeast of Tucson, altitude 1372 m., or 4500 feet) the foliar transpiring power of the two forms *Rhus aromatica* var. *mollis* (Gray) Ashe and *Arctostaphylos pungens* H. B. K. was determined during the twelfth hour, September 8, 1912. The two shrubs were growing within a few meters of each other. The first named is characterized by gray bark, hairy shoots, and rather large, thin, lobed leaves of a strikingly mesophytic aspect; the other is one of the characteristic manzanitas with brownish red bark, smooth shoots and smaller, much thicker, entire leaves of strikingly xerophytic aspect. The results of the tests follow.

Rhus aromatica var. *mollis*

LEAF SURFACE	TIME	INDEX
	<i>seconds</i>	
Upper.....		Not determined
Lower.....	85	0.160
Water test (saturated paper).....	14	

Arctostaphylos pungens

Upper.....	692	0.020
Lower.....	139	0.098
Entire.....		0.059 (average)
Water test (saturated paper).....	14	

The hygrometric paper failed to lose all its blue color on the upper surface of the leaves of the apparently mesophytic form, and consequently an index of transpiring power cannot be obtained for this surface by the present method. It is clear, however,

that the lower leaf surface of this same plant possessed a much greater transpiring power at the time of observation than did the lower leaf surface of the xerophytic form. The lower foliar surface of the latter plant exhibits transpiring power about five times as great as that of the upper surface of the same leaves.

Experiment IX. On September 8, 1912, tests of the foliar transpiring power of *Sphaeralcea pedata* Torr. were made above Oracle, and on the following day the same tests were applied to sensibly similar plants at the Desert Laboratory. The plants were vigorous and in bloom in both cases and were of about the same size. The leaves were apparently alike at both localities, large, thin and practically without hairs, these tests being per-

TABLE 6
Sphaeralcea pedata

LEAF SURFACE	TIME		INDEX OF TRANSPIRING POWER		
			ACTUAL		RELATIVE ORACLE, INDEX AS UNITY
	Oracle	Des. Lab.	Oracle	Des. Lab.	Des. Lab.
	<i>seconds</i>	<i>seconds</i>			
Upper.....	36	44	0.378	0.289	0.76
Lower.....	29	42	0.469	0.302	0.64
Entire.....			0.424	0.296	0.70
Watertest (saturated paper)	14	13			

formed at the end of the summer rainy season.¹² The results of the two tests are presented in table 6, which explains itself. In both cases, the data apply to hour 13.

It is clear that the indices of transpiring power are lower for the Oracle plants than for those at the Desert Laboratory. The average index for the two leaf surfaces is 30 per cent lower for the plants at the higher station than for those at the lower. This is obviously due to a greater difference (36 per cent) between the indices for the lower surface and a smaller one (24 per cent)

¹² In the dry season the leaves of this species are markedly different from those produced with low evaporation rates; in May and June the plants are characterized by small, thick, densely hairy leaves. In this connection see the following paper: Livingston, B. E., Evaporation as a climatic factor influencing vegetation. Horticultural Society of New York. Memoirs 2: 43-54, 1910.

between those for the upper surface. In spite of pronounced differences in appearance, the two leaf surfaces at the lower station possessed almost identical indices of transpiring power. At the upper station these two indices differ widely.

CONCLUSIONS

As has already been pointed out, the method of the hygrometric paper tests promises to be of value in the determination of the diurnal fluctuations in the transpiring power of many plant surfaces, and appears to furnish at least a possible and practicable alternative to the method of the relative transpiration ratio. In this particular the new method is available in purely scientific studies, whereby the causal relations between external and internal conditions are to be established and fundamental principles are to be sought.

Also the new method puts it in the power of the student approximately to measure and compare the internal conditions of different plants, or of the same plant at different times, in regard to one very important feature of the exceedingly complex water relation. In certain respects the criterion of transpiring power should be at least as valuable in plant comparisons as are those of color, form, size, etc., upon which the descriptive botany of the past has almost wholly relied. Here appears to be a simple means by which to compare certain physiological possibilities of different individuals or forms.

One of the main points in regard to which the method of the standardized hygrometric paper is to be regarded as a forward step, lies in the fact that it makes possible the study of the relative transpiring power in the case of plants growing in the open soil. That the results are confessedly only roughly approximate and that the method itself is somewhat tedious in application, are not facts of primary importance when it is remembered that the relative transpiration ratios, always derived from potted plants or cut portions of plants, have heretofore furnished our only satisfactory means for acquiring quantitative knowledge of the power of plant surfaces to supply water to the aerial surroundings.

Turning now to the results of the series of selected experiments which precedes the present section, we note that the transpiring

power of the leaves of *Physalis* and of *Datura* (experiments I and II), grown in pots as already described, exhibits a diurnal march or fluctuation, from a low value in the night hours to a much higher one in the day. A similar condition of affairs is suggested in the case of the two observations upon *Ruellia* (experiment V). Furthermore, the diurnal fluctuation in foliar transpiring power of the three forms just mentioned is the resultant of very different fluctuations in the separate transpiring powers of the two leaf surfaces. Variations in this feature are not at all the same for the two leaf surfaces as for the leaf as a whole; the two surfaces may alter in this respect either more or less rapidly than does the entire leaf surface, or one of them may actually vary in the opposite direction. While there is evidence that stomatal distribution and movements may account for these fluctuations in many cases, there is evidence also that some other condition is frequently of prime importance. There appears no logical ground for doubting that the phenomenon recently called *incipient drying* by Livingston and Brown (loc. cit.) plays an important rôle in the determination of the fluctuations here considered, but the time is not ripe for a thorough treatment of this problem.

As to the actual magnitudes of the indices of foliar transpiring power given in the present paper, it will be instructive to summarize these in table 7. The data are rounded off with the third place of decimals. The indices corresponding to the minimum and maximum transpiring powers of the entire leaf surface are given for the first two plants. The lowest index in the table is the indeterminate one for the upper leaf surface of *Rhus aromatica* var. *mollis*, and the lowest determinate one is 0.009, for the lower surface of *Physalis* at 22 hours. Following the indices for the separate leaf surfaces are placed numbers in parentheses, these numbers indicating the order of magnitude of the index, in the series given in the table. The indices for the entire leaf surface are not considered in this numbered series.

While there are a number of cases in which the two indices for a given observation occur in the same region of the numbered series, e.g., *Martynia* (28, 29), *Zea* (13, 12), *Sphaeralcea*, Oracle (25, 27), etc., yet there are also cases wherein the two simultane-

ous indices are very widely separated in the numbered series, e.g., *Ruellia* (4, 19), *Sorghum* (8, 24), *Rhus* (1, 20), etc.

The total range of the series of indices is surprisingly great, from 0.009, and below, to 0.760. One leaf surface could supply moisture to the air over seven-tenths as fast as a water surface blanketed by a millimeter of air and another could supply it only nine-thousandths as rapidly as this water surface.

The data here given are to be regarded merely as a series of more or less representative samples of the indices of transpiring

TABLE 7

PLANT	TIME AND PLACE OF OBSERVATION	INDEX OF TRANSPIRING POWER		
		Upper leaf surface	Lower leaf surface	Entire leaf surface
<i>Physalis</i>	22 hrs., July 25, 1911, Tucson	0.020 (4)	0.009 (2)	0.014
	12 hrs., July 26, 1911, Tucson	0.072 (14)	0.112 (18)	0.092
<i>Datura</i>	24 hrs., Sept. 3, 1911, Tucson	0.027 (5)	0.016 (3)	0.021
	15 hrs., Sept. 2, 1911, Tucson	0.295 (22)	0.453 (26)	0.374
<i>Martynia</i>	11 hrs., Sept. 17, 1911, Tucson	0.680 (28)	0.760 (29)	0.720
<i>Zea</i>	11 hrs., Sept. 17, 1911, Tucson	0.064 (13)	0.061 (12)	0.063
<i>Phaseolus</i> , pri- mary leaves...	17 hrs., Sept. 9, 1911, Tucson	0.031 (6)	0.108 (17)	0.070
Secondary leaves	17 hrs., Sept. 9, 1911, Tucson	0.053 (11)	0.112 (18)	0.083
<i>Ruellia</i>	23 hrs., Sept. 12, 1912, Tucson	0.038 (8)	0.033 (7)	0.036
	16 hrs., Sept. 12, 1912, Tucson	0.020 (4)	0.124 (19)	0.072
<i>Nicotiana</i>	12 hrs., Sept. 1, 1912, between Tucson and Oracle	0.052 (10)	0.094 (15)	0.073
<i>Sorghum</i>	4 hrs., Aug. 31, 1912, Tucson	0.043 (8)	0.303 (24)	0.173
<i>Rhus</i>	12 hrs., Sept. 8, 1912, Oracle	(Indeterm. very low) (1)	0.160 (20)	
<i>Arctostaphylos</i> ...	12 hrs., Sept. 8, 1912, Oracle	0.020 (4)	0.098 (16)	0.059
<i>Sphaeralcea</i>	13 hrs., Sept. 8, 1912, Oracle	0.378 (25)	0.469 (27)	0.424
	13 hrs., Sept. 9, 1912, Tucson	0.289 (21)	0.302 (23)	0.296

power which occur in the plant kingdom. Many more tests will have to be carried out before reliable generalizations may be attempted, but it seems clear that we have before us evidence enough to warrant the further prosecution of this line of inquiry.

Students of ecology have devoted many hundreds of pages to attempts toward a classification of plants on the basis of their water relations, using as criteria almost wholly the more or less superficial appearance, on the one hand, of the habitats in which

the various forms naturally occur, and, on the other, the appearance of the plant itself (including of course its internal as well as its peripheral structures and characters). That the character of its place of occurrence cannot satisfactorily be used in the definition of a natural object—whether this be an element, a mineral or an organism—is a principle which gains in prominence with the advance of every branch of science, and it appears that the growth of plant ecology may soon lead to the dynamic or physiological study of the organism, as offering the only really useful criteria for ecological classification. In so far as the attempted classification is to be based on the water relation (and all far-reaching attempts toward such classification have been so based, *e.g.*, those of Warming, Schimper and others), it appears that there are just three features of the plant that need to be involved in an adequate ecological description. These three features are (1) the power of the plant to absorb water from its surroundings, (2) its power to distribute absorbed water within its body and (3) its power to prevent the loss of water to its surroundings; all other features are negligible in a classification based upon the water relation.¹³ We are still very far from the possession of any well-tried means for studying the first two features just mentioned, but the method of relative transpiration and that of the index of transpiring power do seem to furnish a means at least temporarily adequate for the study of our third feature, and this is the main point with which this paper has had to deal. A statement of the limits of variation of the index of transpiring power of a given plant should be much more satisfactory than its mere reference to an ill-defined category such as that of xerophytes, etc.

It may be suggested finally that the conception of transpiring power (or its reciprocal, resistance to water loss by transpiration), together with the somewhat widely applicable method of hygrometric tests, should prove of great practical value to students of agriculture. We should now be able to distinguish, physiologically and quantitatively, in so far as their aërial water relation is concerned, between different varieties of cultivated plants.

¹³ For an outline of the main features of the water relations of plants, see: Livingston, B. E., A schematic representation of the water relations of plants. *Plant World*, 15: 214-18, 1912.

A NOTE ON A CHAPARRAL-FOREST RELATION AT CARMEL, CALIFORNIA

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In the vicinity of the Carmel, California, branch of the Desert Laboratory there are many land and sea plants which are of much interest, not only in or of themselves, but, also, in the relationship which they often hold to each other. The present note refers to certain features in the relations between chaparral and forest which came to my attention recently.

On the Monterey peninsula, which lies between Monterey bay and Carmel bay, and in the vicinity of Carmel, as well as in the town itself, the most important formations of the larger land plants are forest and chaparral. The forest is composed almost entirely of *Pinus radiata* and *Quercus agrifolia*, with the former dominating. There are also Monterey cypress (*Cupressus macrocarpa*), *Cupressus goveniana*, *Pinus muricata*, *Quercus wislizenii*, *Quercus agrifolia*, and other oaks, but all of these are of restricted range, or occur in small numbers. The relation of the oaks to the pines is a peculiar one and will not be touched on here.

The chaparral may be found in the Carmel region ranging from 100 feet to 2000 feet, and may reach within one-half mile, or so, of the sea. At the higher altitude it occurs free of forest trees, and there one finds such shrubs as *Garrya*, *Ceanothus*, *Vaccinium*, *Custaniopsis*, *Adenostoma*, *Arctostophylos* and others. At the lower altitudes, however, the chaparral may not be free from forest intrusion. This is the condition at Carmel where the Monterey pine (*P. radiata*) and Eucina oak (*Quercus agrifolia*) especially invade the chaparral, forming an open forest with the pine dominating. There are no apparent differences in the sub-aërial portions of such pines as develop in chaparral and such as grow free from chaparral, but it is possible, from what will

be given presently, that the root-systems of pines of the two habitats show some variation.

In the course of changes which have accompanied the establishment and subsequent growth of the town of Carmel several instances have been noted where the chaparral has been removed, leaving the pines and oaks otherwise undisturbed. In such cases the clearing off of the chaparral has been followed, after a lapse of two years, more or less, by the death of the pines.

In considering the possible causes which bring about the death of the pines it would be noted that the species has at least two insect enemies, one of which is a serious menace. There is a fly which attacks the leaf buds in early spring with the result that subsequent leaf development is abnormal,¹ and a beetle, which penetrates the bole to the cambium, often girdling the tree and interfering with the movements of sap and sometimes causing death. In the present case, however, neither of these causes need be considered as contributing in a material way to the result noted above. The probable conditions, leading to the death of the pines, are as follows. These are in part climatic and in part accidental, being related to environmental changes induced by the presence of the chaparral during the development of the pine and by the subsequent removal of the chaparral.

The main features of the climate of Carmel, so far as they touch the present topic, have to do with the amount and the character of the rainfall. Precipitation occurs in the winter months mainly, the summer months being without rain. The average rainfall is over 18 inches. Fog serves to ameliorate the summer dryness along the coast, which, however, is fairly arid. Among other results the long dry period brings about the drying out of the soil to such a degree, especially away from the fog belt, that most annuals are dormant.

The chaparral is sufficiently dense to completely cover the ground and affords a certain and large degree of protection against excessive drying out. The protection thus given to the ground, by which a disastrous desiccation is prevented, disap-

¹ Cannon, W. A.: The gall of the Monterey pine. *Am. Nat.* **34**: 801-810, 1900.

Peirce, G. J.: Notes on the Monterey pine. *Bot. Gaz.* **37**: 448-455, 1904.

pears with the complete and sudden removal of the chaparral. This is shown by the disappearance of much of what herbaceous growth is characteristic of this formation with its destruction, and, as we have seen, by the death of the pines, under conditions to be given directly.

The roots of the Monterey pines, so far as has been observed, are in part very shallowly placed. Long and large roots of mature plants lie close to the surface of the ground and are often in part uncovered by the rains. In old trees these roots serve in part for mechanical support, but the absorbing roots are also in part superficially placed. The laterals of the young pines extend outwards from the main axis for a comparatively long distance and lie mainly within 6 inches of the surface. The roots are so well developed that the transplanting of trees grown in nature is difficult except in the very young specimens. From observations made on the roots of the species, therefore, it appears that changes in the water relations of the upper soil layers may be of importance in the survival of the individual. This conclusion is of especial significance when the long summers' rainless character of the climate is taken into account.

The leading events which bring about the death of mature pines, therefore, under conditions given above, may be briefly given. The chaparral affords a protection to the soil against excessive drying out in summer. The root-systems of pines which invade the chaparral adapt themselves in position to this, and when the chaparral is removed, the more arid soil in which the roots find themselves does not yield adequate water supply. Starvation is the ultimate result. Support is given this hypothesis in the springing up and thriving of the younger pine generation, after the cutting of the chaparral.

BOOKS AND CURRENT LITERATURE

A BIOLOGICAL TEXT.—The task of covering the field of Biology has been taken up from a new view point in the Biology prepared by Conn.¹ The author aims to add the consideration of the "broader fundamental laws which should correlate the phenomena of life as one science" to the elementary work in botany and zoology of the secondary schools. As a matter of fact however the manner of treatment does not get rid of the circumstance that plants and animals are different types of organisms, although more emphasis is placed upon the physiological principles common to both, than is frequently the case. After discussing the general field, and the position of unicellular organisms, examples of multicellular plants and animals are taken up in an ascending order; the Castor Bean, *Hydra*, *Lumbricus*, and *Rana* being the types selected. The morphology, and the physiology of these are discussed, then the two types of organism—plant and animal—are contrasted in general and in respect to reproduction and developmental history. Finally, four chapters are given to theoretical discussion of the questions related to the Source of Energy, the Living Machine, Origin of Organisms, and Evolution, with a final chapter on Classification.

The book has been prepared for college students, apparently of the Sophomore year, in anticipation of specialization in either Botany or Zoology later. But the text itself is not uniform in style, parts being written as if for secondary students, and other parts as if for Junior men with laboratory work. An enumeration of the numerous bones in the limbs of the frog, does not have any added information beyond that supposed to have been received in the secondary school course. The advantage of short bones in a clasping or supporting organ, like the hand or foot, is not mentioned, or hinted at. The details of chromosome divisions in the maturation of the egg and sperm cells are given as if for senior classes, but the relative size of the cells as finally formed is lost through the faulty execution of the drawings intended to show them. In an effort to cover two distinct fields, as in this case, one is

¹ Conn, Herbert W., Biology: An Introductory Study, for use in Colleges. Pp. 425. Silver, Burdett and Company, New York, 1912 (\$1.50).

very apt to allow words to pass which would not be chosen if writing for a more restricted group of readers. While the general truths hold as stated, the details are often in error, according to the usual use of words, as when proteids are said to be "eliminated" in the seeds and falling leaves of plants. The reviewer regrets to see so much effort placed on a text covering a field which has been outgrown by its component parts. Biology, like Microscopy, has developed into intensive study, and can not be satisfactorily covered in a single text.

FREDERICK H. BLODGETT.

BACTERIA IN FROZEN SOIL.—Work by Brown and Smith is in part a confirmation of that of Cohn relative to the existence of specific groups of bacteria which are capable of living and rapidly multiplying in frozen soils.¹ A seemingly plausible explanation for this condition is that the films of hygroscopic water become more concentrated as the main body of soil water freezes, thus depressing the freezing point so that the hygroscopic moisture may remain uncongealed. Then, too, it is a well known fact that the pressure exerted in holding the film around the soil particles is sufficient to lower the freezing point of the hygroscopic water below zero degrees Centigrade. The evidence which the authors adduce indicates that frozen soils possess a much greater ammonifying power than non-frozen soils. Frozen soils possess a weak nitrifying power but a decided denitrifying power which diminishes as the cold continues. There is, as the frozen period continues, an increase in the nitrogen fixing power of frozen soils, the fixation being less, however, than in the fall season.—FREDERICK A. WOLF.

EVAPORATION IN ILLINOIS.—Gleason and Gates have published the results of their study of relative evaporation in central Illinois.² The plant associations investigated range from the "blowout" association in loose sand to the mixed forest, which is the local climax of the uplands about Havana. The results are represented in terms of an arbitrary standard as follows: blowout 1.27–1.56, bunchgrass 1.04–1.18, beach (along Illinois River) 0.93, black oak 0.55–0.66, willow 0.44–0.56, mixed forest 0.29–0.36. The authors conclude that the difference in the various associations is due principally to the nature of the vegetation.

¹ Brown, P. E. and Smith, R. E.: Bacterial activities in frozen soils. Iowa Agr. Exp. Sta. Res. Bull. 4: 159–184, 1912.

² Gleason, H. A. and Gates, F. C.: A Comparison of the Rates of Evaporation in Certain Associations in Central Illinois. Bot. Gaz. 53: 478–491, 1912.

They find the highest rates of evaporation in the initial stages of both the prairie and forest successions. They believe "the observations indicate that successions between associations are not caused by any condition of evaporation." This last statement is not easily reconciled with the others, since successions are directly due to the survival of seedlings and the rate of evaporation must be very important in this connection. —E. N. T.

VEGETATION OF NATAL.—Bews has published a brief account of the climate and vegetation of Natal, with some excellent illustrations.¹ The coastal bushland is of tropical floristic composition, the midland is less tropical but like the coastal in being dominated by evergreen broad-leaved trees; the bush of the interior is largely made up of *Podocarpus*. The greater portion of the interior is occupied by thorn veld, a savannah formation, and by high-level or low-level veld, as the author designates the commonest types of grassland. The ingenuous supposition that the trees of the thorn veld might occupy spots with a greater soil moisture than the grass-covered intervals between them led to the discovery of a uniformly low moisture content. The prevention of veld fires (and apparently of grazing also) results in an increased stand of trees in the thorn veld. A large body of well presented climatological data throws a small amount of light on the distributional features of the vegetation. —F. S.

¹ Bews, J. W.: The Vegetation of Natal. Ann. Natal Mus. 2: 253-331; pls. 14-23, 912.

NOTES AND COMMENT

During the years in which the national Forest Service has been undergoing rapid growth and development, its leaders have become increasingly aware of the necessity of a broad foundation of scientific principles for the regulation of its manifold technical activities. The forest crop of the United States is almost as varied as its agricultural crop, and its production is conditioned by quite as great an array of determining factors. The agricultural crop is produced speedily, usually in a few months, and is from the start a product of the activity of man; the forest crop is the growth of decades or of centuries, and its inception has usually taken place under natural conditions. These circumstances are to be held accountable for the tardiness with which foresters, as compared with agriculturists, have come to recognise the value of scientific investigation in laying secure foundations for their work. The Report of the Forester for 1912 calls attention to the steps which have been taken by the Forest Service to promote the carrying out of experimental work in reforestation and "forest influences" as well as in forest management, fire protection and other more practical matters. A central committee has been appointed to supervise the investigation, to determine the lines of work which are most urgent, and to prevent unnecessary duplication of work within the Service. The actual researches are being carried out at a series of Forest Experiment Stations, which are to all intents and purposes close analogues of the agricultural experiment stations, with differences due to the dissimilarity of the end products of these two great branches of applied botany, and to the slowness which the longevity of trees imposes on experimental work with the forest crop.

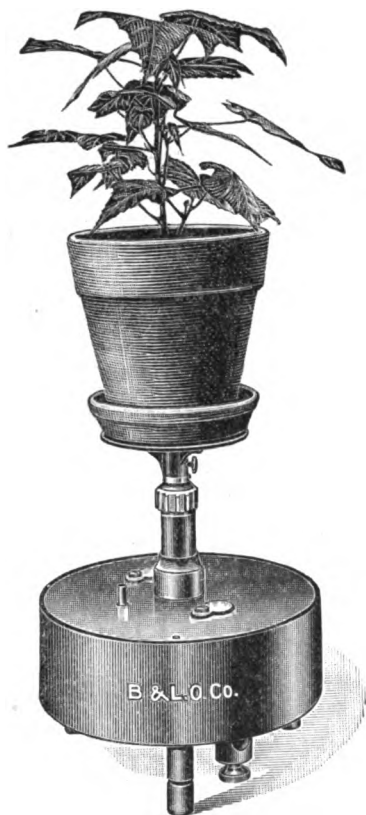
Six Forest Experiment Stations are now in operation at widely separated localities in western National Forests, and coöperative work is being carried on in two other places. The oldest of these is the Fort Valley Experiment Station, established in 1908 and located in the Coconino Forest in northern Arizona. The group of problems with which this station is concerned center about the reproduction of the western yellow pine, the chief commercial tree of the national forests of Arizona and New Mexico. Seed production and viability, natural reproduction, and nursery and planting methods have already been

studied, and work is now in progress on the influence of soil moisture, wind, and light on the reproduction and establishment of the yellow pine. An additional investigation under way is one looking to the possibility of securing turpentine from the western yellow pine. The attack upon these difficult and important problems is being made in a most thorough and comprehensive manner by the present officer in charge. In 1909 two more stations were established, the Fremont Forest Experiment Station, in the Pike National Forest, Colorado, and the Wagon Wheel Gap Station, in the Rio Grande Forest, Colorado. The work of the Fremont Station is looking to a determination of the environmental factors which underlie the occurrence of different types of forest. The investigations thus far prosecuted have been concerned with the soil and climatic differences between habitats dominated respectively by Engelmann spruce, Douglas fir, and yellow pine. The results indicate at present that soil moisture and soil temperature are the chief controlling and differentiating factors involved. At this station also the most thoroughgoing methods are being employed, and the attainment of the full value of the work under way is not expected for many years to come. At the Wagon Wheel Gap Station a more practical problem is under investigation, the outcome of which will give quantitative details regarding facts which are already well known. Two valleys have been selected which are alike in all their natural features, and concrete dams have been erected in the principal streamway at the foot of each of the areas. The rainfall and stream flow of the valleys are to be measured for two years, one of the areas is then to be denuded of forest and the influence on stream flow to be determined. The observations on the difference between the climatic conditions and run-off of the two areas will be continued during the natural reforestation of the denuded area. The Utah Forest Experiment Station, on the Manti National Forest, Utah, is concerned with practical problems in regard to the best methods of restoring grasses and shrubs in overgrazed forests. The Feather River Station, in the Plumas National Forest, California, and the Priest River Station, in the Kaniksu Forest, Idaho, have been but recently established and nothing has been heard of their operations.

We venture to predict that the work of these stations represents merely the beginning of a large body of activities which will ultimately place the practise of forestry in America on a most enlightened and efficient scientific basis.

The University of Minnesota has just issued the Ninth Report of the State Botanical Survey: a Manual of Minnesota Trees and Shrubs, by Professor Clements, Professor Rosendahl, and Assistant Professor Butters, of the University staff. The book will be useful to residents of Minnesota by reason of its keys and numerous illustrations, and to botanists at large through its detailed statement of the range and limits of trees in that state.

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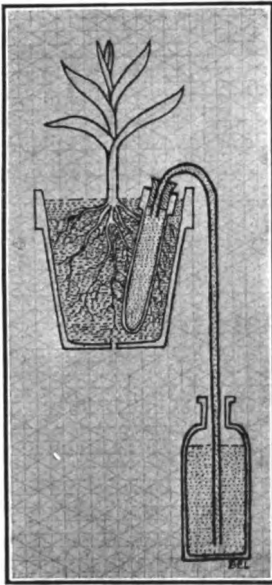
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Plant World, Vol. 11, pp. 39-40, February, 1908.

Plant World, Vol. 13, pp. 220-227, September, 1910.

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